

POTENTIAL ADAPTABILITY AND
CONSTRAINTS OF RESPONSE TO
CHANGING CLIMATES FOR
ENCELIA FARINOSA VAR. *PHENICODONTA* FROM
SOUTHERN BAJA CALIFORNIA, MEXICO

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ABSTRACT

To examine the physiological adaptability of *Encelia farinosa* var. *phenicodonta* from southern Baja California, plants from Todos Santos, BCS were raised in central Arizona where winter-spring precipitation is greater than typically experienced by this variety. Plants were capable of high photosynthetic rates during the cool and wet spring months and showed substantial growth and reproductive output. Winter freezes caused severe stem dieback and even plant death. These findings suggest that freezing temperatures may influence the restricted and disjunct distribution of *E. farinosa* var. *phenicodonta* in the northern part of its range. The growth and reproduction results also imply that this variety may possess the physiological adaptability to thrive under potential climatic changes in southwestern North America.

RESUMEN

Para evaluar la adaptación fisiológica de *Encelia farinosa* var. *phenicodonta* del sur de Baja California, plantas de Todos Santos, BCS, fueron cultivadas en centro Arizona donde la precipitación de invierno y primavera excede la experimentada normalmente por dicha variedad. Plantas de BCS fueron capaces de altas tasas de fotosíntesis aún durante los lluviosos y fríos meses de primavera y además mostraron un incremento substancial en crecimiento y reproducción. Sin embargo, heladas de invierno causaron la muerte de tallos y en un caso severo toda la planta. Estos resultados sugieren que frías temperaturas de invierno pueden influir la distribución de *E. farinosa* var. *phenicodonta* en la parte norte de su presente rango de distribución. Estos resultados también sugieren que esta variedad posiblemente posee la adaptabilidad fisiológica para prosperar ante los posibles cambios climatológicos en el suroeste de Norte América.

Encelia farinosa A. Gray (Compositae) is a ubiquitous drought-deciduous perennial shrub of southwestern North America. Three varieties have been described based on variation of flower color and leaf morphology (Shreve and Wiggins 1964), and the distributions of these taxa are only somewhat sympatric (Kyhos 1971; Hastings et al. 1972). *Encelia farinosa* var. *farinosa* is most common throughout the Mojave and Sonoran deserts of California, Arizona and So-

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nora. *Encelia farinosa* var. *radians* Brandege ex S. F. Blake the rarest of these varieties, is restricted to the Cape region of Baja California. *Encelia farinosa* var. *phenicodonta* (S. F. Blake) I. M. Johnst. is widespread throughout central and southern Baja California, but its northern distribution is mostly restricted to the Colorado River drainage and tributary regions within Arizona and California (Fig. 1).

Studies of variation in ecophysiology and water use have been conducted for many years with *E. farinosa* var. *farinosa* (Shreve 1923; Cunningham and Strain 1969; Ehleringer and Mooney 1978; Smith and Nobel 1978; Ehleringer and Cook 1990; Monson et al. 1992). These studies have shown that *E. farinosa* var. *farinosa* is a highly adaptable taxon that can exhibit genetic differentiation over short topographical gradients (Monson et al. 1992) as well as local adaptation on broader geographic scales (Ehleringer 1985; Ehleringer and Cook 1990). Much less is known about the conspecific *E. farinosa* var. *phenicodonta* despite its widespread distribution in Baja California and its unusual distribution in California and Arizona.

Kyhos (1971) suggested that the scattered populations of *E. farinosa* var. *phenicodonta* in its northern range may be remnants of a once broader distribution that existed during a warmer, more mesic period. Hence, *E. farinosa* var. *phenicodonta* may be predisposed to expanding its range if, as predicted by Schlesinger and Mitchell (1987), the Mojave and Sonoran desert regions eventually experience warmer temperatures and enhanced summer rainfall. However, such range expansion would extend *E. farinosa* var. *phenicodonta* into regions with much greater winter-spring precipitation than typically found in its current range, and in these northern desert regions winter-spring rainfall is predicted to remain at present amounts or even increase in the future (Schlesinger and Mitchell 1987).

To better understand the adaptability of *E. farinosa* var. *phenicodonta*, we examined the physiology and phenology of plants from southern Baja California, Mexico, when grown under winter-spring conditions that are atypical of that region. By raising these plants in central Arizona, we could address simple questions about the lability of physiological responses and general constraints that may affect the distribution of this taxon. This study focused on the physiological capacities for exploitation of winter and spring rainfall, and growth and reproduction in these cooler seasons. In addition, we observed phenological responses to freezing because freeze-tolerance is an important climatic factor limiting the northern distribution of many desert species (Shreve 1914; Jones 1978; Bowers 1981), and *E. farinosa* varieties have been shown to be sensitive to low temperatures (Tumage and Hinckley 1938; Hastings and Turner 1965; Jones 1978).

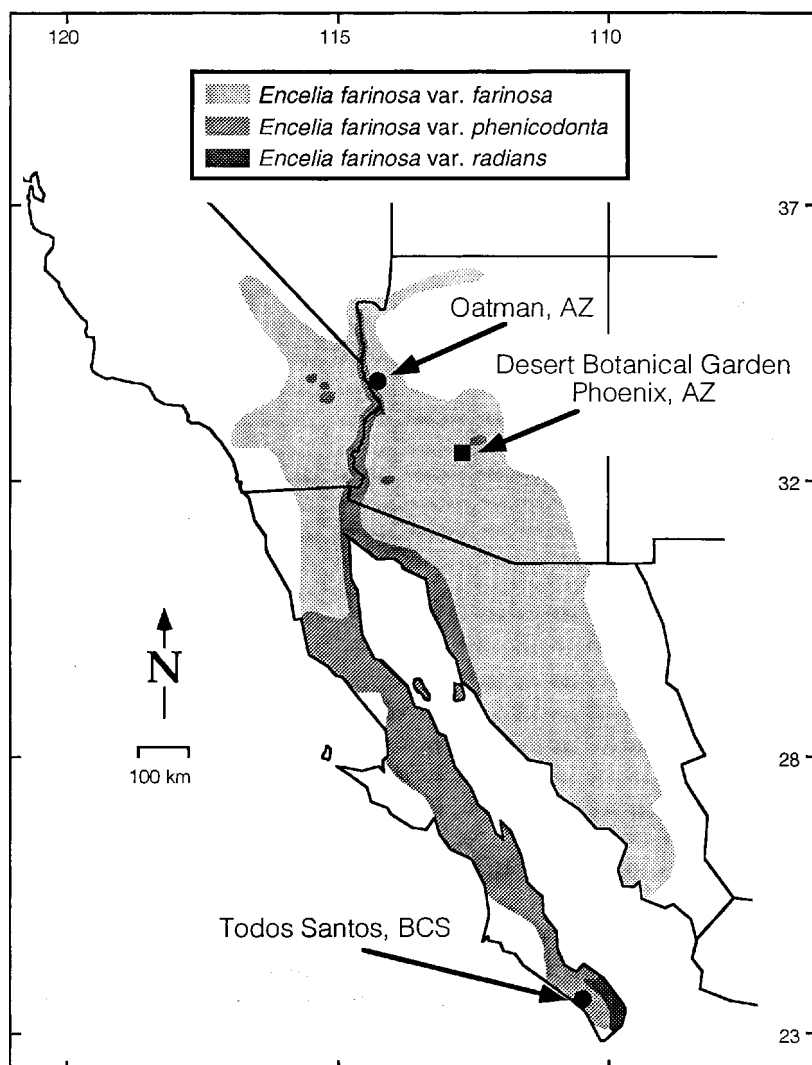


FIG. 1. The distributions of *Encelia farinosa* varieties in southwestern North America (adapted from Kyhos 1971; Hastings et al. 1972). Also shown are the sites of seed collections and the Desert Botanical Garden, where the research took place.

METHODS AND MATERIALS

Seeds and leaves of *E. farinosa* var. *phenicodonta* were collected in October 1989 from a natural population near Todos Santos, Baja California Sur, Mexico (23°26'N, 110°14'W, 18 m) (Fig. 1). The

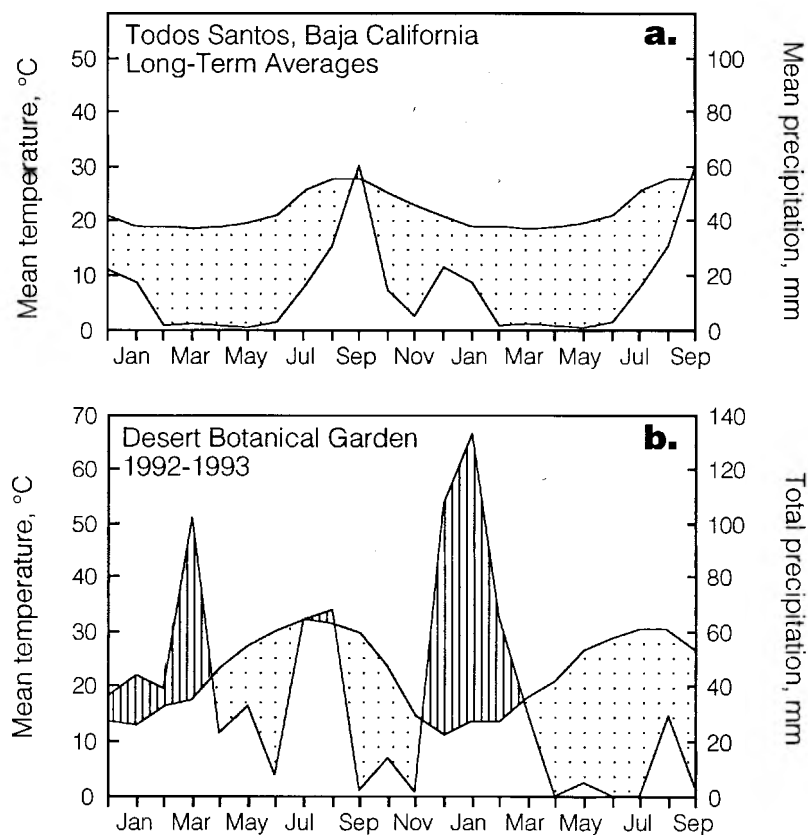


FIG. 2. Climate diagrams of monthly temperature and precipitation data. Stippled areas are periods of relative water deficit; striped are periods of water surplus. a) Long-term averages for Todos Santos, Baja California Sur, MX (1921-1967; data from Todos Santos weather station; Hastings and Humphrey 1969). b) Desert Botanical Garden monthly values from December 1991 to September 1993. Data are from the Tempe, Arizona, USA weather station, 2 km SW (Arizona Climate Summary, Office of the State Climatologist for Arizona).

long-term mean annual rainfall at Todos Santos is 170 mm (Hastings and Humphrey 1969). Of this, only 3% comes between the months of February and June (Fig. 2a), and during these months plant activity is normally very limited (Shreve 1937).

Seeds were germinated at the University of Utah greenhouse in September 1990 and transplanted to the Desert Botanical Garden in Phoenix, AZ (33°30'N, 112°00'W, 360 m) on 31 March 1991. The Desert Botanical Garden (DBG) is within the natural range of *E. farinosa* (Fig. 1) and gravelly soils at DBG are typical of *E. farinosa* habitat.

Monthly precipitation and mean temperatures at DBG during the two years of this study are shown in Figure 2b. Rainfall in the winter and spring months of 1992 and 1993 was very high. On average this input was seven times greater than normal for Todos Santos. Summer precipitation at DBG in 1992 was about the same as the long-term average at Todos Santos, but in 1993 rainfall was virtually absent from April through August (Fig. 2b).

Summer and autumn temperatures at DBG were comparable to Todos Santos averages (Fig. 2), but winter temperatures were relatively low. Recent weather records from the La Paz airport (La Paz, Baja California Sur, MX), 71 km N of Todos Santos, show that there had only been one day with a sub-freezing temperature in the past 15 years and the average minimum temperature in January, the coldest month, is 12.2°C (National Climatic Data Center, Asheville, NC). At DBG in winter 1992–1993 there were three December days with a minimum temperature below 0°C, two of which were consecutive. The average minimum temperature in December 1992 (4.3°C) was 1.9°C greater than the long-term average. The following winter had subfreezing temperatures on 26 days between 4 December 1993 and 3 February 1994, and during this period there was one seven-day period of <0°C minimum values. The average minimum temperature for December and January was 0.6°C, which, on average, was 2.7°C below the long-term mean (Arizona Climate Summary, Office of the State Climatologist for Arizona).

Twenty plants used for this study were randomly chosen from within a 26 m × 26 m plot of *E. farinosa* plants. All plants were separated by 2 m, a sufficient distance to preclude root interactions among plants (Ehleringer 1984), and the plot was bordered by a single row of non-experimental *E. farinosa*.

Surveys began with phenological and developmental measurements on 28 February 1992 and were repeated approximately every 60 to 90 days through 24 August 1993. Plant water status and gas exchange measurements were made from March through the last sample date of each year, with a few exceptions. Predawn leaf water potentials (ψ_{pd}) were measured on one or two leaves per plant with a Scholander-type pressure chamber (PMS, Corvallis, Oregon). Measurements were taken within the 3-hour period prior to sunrise. Stomatal conductance (g), which affects both water loss and carbon assimilation, was measured in conjunction with net photosynthetic rate (A) during the 2–4 hours after sunrise. These hours are during maximum photosynthetic activity for *E. farinosa* (Ehleringer 1988). Measurements of g and A were made on a single leaf or group of leaves using a LiCor 6200 portable gas exchange system (LiCor Inc., Lincoln, Nebraska). Leaves used for all measurements were from the most recent, fully expanded leaf cohort and were always in the southeast part of the upper plant canopy.

Carbon isotope composition was measured for leaves collected at Todos Santos in October 1989, and for leaf samples collected at DBG in September 1992. The carbon isotope ratio of a leaf (δ_p) is inversely related to the intercellular concentration of CO_2 during photosynthesis (c_i) (Farquhar et al. 1989), and for *E. farinosa*, c_i is genetically correlated with stomatal conductance (D. R. Sandquist, unpublished). Thus δ_p can be used to infer g values for a leaf (Farquhar et al. 1989).

Leaves were dried and ground, and carbon isotope ratios were determined relative to the Pee Dee Belemnite standard (Ehleringer and Osmond 1991). Analyses were done at the University of Utah Stable Isotope Ratio Facility for Environmental Research with Delta E and Delta S mass ratio spectrometers (Finnigan-MAT, San Jose, CA). Values are reported as isotope ratios (δ) in the per mil (‰) notation. The overall, long-term error associated with carbon isotope determination is $\pm 0.11\text{‰}$.

Plant height, maximum width and width perpendicular to the maximum width were used to calculate plant volume based on the equation for a half spheroid. Foliage density (m^2m^{-3}) of a plant was determined from a non-destructive estimation of the canopy leaf area (m^2) divided by plant volume (m^3). Canopy leaf area was estimated from an extrapolation based on the leaf areas of three leaves per each of three stems that were subjectively chosen to each represent one-third of the plant canopy (Appendix 1). The presence or absence of flowers was recorded throughout the study, and the number of flower heads produced per plant was counted in April 1992, the peak of flowering during that year.

Plant damage due to freezing during winter 1992–1993 was estimated on 30 January by visual inspection of the proportion of stems that lost apical dominance. Loss of apical dominance, if present, was very distinct since leaves near the stem tips had died and axillary branching had already started. The following winter, freeze damage was assessed in February 1994 using a different index since all plants had suffered 100% loss of apical dominance. Based on regrowth, plants were ranked as: 0) “killed”, known to have occurred over winter, 1) “extreme damage”, indicated by having only basal regrowth and no active mature stems, 2) “major damage”, indicated by regrowth on $<50\%$ of mature stems, 3) “moderate damage”, regrowth on $>50\%$ of mature stems, 4) “minor damage”, all mature stems still active. In this year 20 additional plants, raised concurrently in the DBG plot but of a different seed source, were surveyed for comparison. These plants were from a northern population of *E. farinosa* var. *farinosa* near the Colorado River drainage and the town of Oatman, Arizona (Fig. 1).

Statistical analyses were performed in JMP 3.1 (SAS Institute

Inc., Cary, NC). Plant volume and flower number were log transformed to normalize distributions.

RESULTS AND DISCUSSION

Winter and spring activity. Precipitation at the Desert Botanical Garden was high from December through March of both years (Fig. 2b), and greatly exceeded the normal winter-spring precipitation of the Todos Santos region (Fig. 2a). Additionally, temperatures at DBG were lower than those typical at Todos Santos.

In 1992, under these wet and cool winter-spring conditions at DBG, Todos Santos plants appeared to be fully active with respect to both productivity and water use parameters (Table 1). High foliage densities and photosynthetic rates indicate that Todos Santos plants have the capacity for high productivity under these conditions.

A similar pattern was seen in 1993. Foliage density and ψ_{pd} was greatest in March (Table 1) but, A and g values increased from March to April. Interpretation of this pattern should be cautious since the increases could have been a response to a late spring rain event (30 mm on 27 March), or a delayed recovery from winter freeze damages (below), or both. Nonetheless, continued growth from March to April 1993 again showed that Todos Santos plants can exploit higher rainfall, and during cooler conditions, than usually experienced in winter-spring.

Maximum photosynthetic rates for *E. farinosa* var. *phenicodonta* in this study (Table 1) were comparable to those for local *E. farinosa* var. *farinosa* measured during a greenhouse experiment (ca. 25–32 $\mu\text{mol m}^{-2}\text{s}^{-1}$, Monson et al. 1992) and in the field (Comstock et al. 1988; Sandquist 1995). Maximum stomatal conductances (Table 1) were also similar to values reported in other studies (ca. 0.4 $\text{mol m}^{-2}\text{s}^{-1}$) of *E. farinosa* var. *farinosa* in central Arizona (Ehleringer and Cook 1990; Monson et al. 1992).

Canopy development and plant sizes were also comparable to those in previous reports. Monson et al. (1992) reported a maximum leaf area per stem just greater than 300 cm^2 . The conversion of our maximum foliage density estimate (March 1992) to leaf area per stem resulted in a similar value, 309 cm^2 (± 43 , 1 SE). In addition, our results showed that plant areas (m^2) after 27 months in DBG (June 1993) were of similar size to *E. farinosa* var. *farinosa* plants grown at DBG under irrigated conditions from 1979 through 1981 (Ehleringer and Cook 1990).

The responses observed during these winter-spring conditions are not necessarily unexpected for a species that is generally water limited. Importantly, however, these results demonstrate that there is no

TABLE 1. SEASONAL CHANGE IN PHYSIOLOGICAL AND PHENOLOGICAL TRAIT MEANS (± 1 SE) FOR SOUTHERN BAJA CALIFORNIAN *ENCELIA FARINOSA* VAR. *PHENICODONTA* RAISED AT THE DESERT BOTANICAL GARDEN, PHOENIX, AZ, USA.

	Predawn water potential (MPa)	CO ₂ assimilation rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$)	Foliage density ($\text{m}^2 \text{m}^{-3}$)	Plant volume (m^3)
Premonsoon 1992					
March	-1.14 ± 0.06	22.0 ± 0.9	0.50 ± 0.04	12.7 ± 1.1	0.034 ± 0.010
April	-1.57 ± 0.09	21.3 ± 1.2	0.50 ± 0.06	10.8 ± 2.0	0.038 ± 0.011
May	-1.81 ± 0.08	19.2 ± 1.7	0.46 ± 0.06	10.4 ± 1.7	na
July	-2.48 ± 0.14	11.4 ± 1.0	0.28 ± 0.04	5.0 ± 0.8	0.042 ± 0.012
Postmonsoon 1992					
August	na	na	na	11.2 ± 0.8	0.077 ± 0.022
September	-1.94 ± 0.13	11.4 ± 0.9	0.20 ± 0.03	5.4 ± 0.3	0.083 ± 0.022
October	-2.54 ± 0.13	10.4 ± 0.8	0.14 ± 0.01	5.1 ± 0.5	0.078 ± 0.021
1993					
March	-0.61 ± 0.03	27.1 ± 0.9	0.67 ± 0.04	8.7 ± 0.8	0.262 ± 0.058
April	-1.02 ± 0.06	30.0 ± 1.2	0.74 ± 0.04	6.9 ± 0.6	0.428 ± 0.064
June	-1.81 ± 0.03	21.2 ± 0.8	0.45 ± 0.03	6.1 ± 0.7	0.507 ± 0.066
July	-2.60 ± 0.11	na	na	3.5 ± 0.3	0.510 ± 0.067
August	na	12.3 ± 0.9	0.32 ± 0.03	2.6 ± 0.3	0.523 ± 0.066

na = data not available.

genetic constraint on the capacity for opportunistic water use and growth under such conditions.

Spring rainfall. The response of Todos Santos plants to spring precipitation was best seen in observations after March 1992, when sporadic rainfall events persisted through the summer (Fig. 2b). In the Todos Santos region, April and May are the driest months of the year, and plant activity is most limited (Shreve 1937; Hastings and Humphrey 1969). Because temperatures at DBG during April and May were near normal for Todos Santos (Fig. 2), the April/May rains provided an opportunity to examine responses of Todos Santos plants to uncommon spring precipitation.

In these months, the downward trend of water potential and other physiological traits continued in spite of substantial water input (Table 1; Fig. 2b). It should be noted, however, that the relative change in ψ_{pd} and foliage density from April to May of 1992 was the least of any consecutive sampling periods in 1992. This may reflect a limited, albeit small, effect of spring rain. Other studies have shown that *E. farinosa* var. *farinosa* plants from the northeastern part of the range responded strongly to late spring rainfall with increased g and A values (Sandquist 1995) and greater foliage densities (Ehleringer 1985; Sandquist 1995). It has also been shown that supplemental watering, after short rainless periods, can raise plant water potential (Ehleringer and Cook 1990; Monson et al. 1992), however, plants from some populations do not respond to late spring rainfall (Ehleringer 1984; Ehleringer and Cook 1990; Sandquist 1995). While Todos Santos plants did not appear to have a substantial response to spring rain, it is clear that they were capable of sustaining activity during unfamiliar climatic conditions and at levels comparable to those reported for native *E. farinosa* plants.

Spring flowering of Todos Santos plants was not apparently constrained. In 1992 only one plant failed to produce flowers, and in 1993 all plants flowered in spring. The average number of flower heads per plant in 1992 was >200 , and flower head production was strongly related to plant size ($R^2 = 0.86$, $P < 0.001$). Because of this relationship there should be a premium on the capacity to grow whenever sufficient water is available. This may explain why there appears to be no seasonal constraint on physiological activities for *E. farinosa* var. *phenicodonta*.

Monsoon season. Pronounced response to monsoon rainfall was expected of Todos Santos plants since this is the period of greatest precipitation in their native habitat. Indeed, mean foliage density increased from a low of $5.0 \text{ m}^2\text{m}^{-3}$ in July to spring-like values of $> 11.0 \text{ m}^2\text{m}^{-3}$ in August, but by September and October the mean foliage density was again back at July levels (Table 1). No data are available for A and g in August, but during the autumn months A

and g also persisted at July-like values (Table 1). September values of Ψ_{pd} , however, remained fairly high and plant volume peaked for 1992 in this month (Table 1).

Summer rainfall is normally high in the Todos Santos region, thus foliage density and A values were expected to be greater than those observed after monsoon rainfall at DBG (Table 1). However, the values seen at DBG may be typical of *E. farinosa* var. *phenicodonta* in southern Baja, where high temperatures and associated water loss constraints could preclude greater values. Although there are no reports for A and g of naturally occurring *E. farinosa* var. *phenicodonta* in the Todos Santos area, we can make inferences from the carbon isotope composition of leaves collected from the same plants used as seed sources for this study. The carbon isotope ratios from these *in situ* plants near Todos Santos averaged -27.9‰ ($SE \pm 0.15$) for October 1989 and were not different from those of plants at DBG in September 1992, $-27.6\text{‰} \pm 0.21$ ($t = 0.94$; $P = 0.35$).

The lack of a difference between δ_p means suggests that g values were the same among these samples; assuming that environmental conditions were similar during leaf development (Farquhar et al. 1989). This assumption is reasonable based on the comparison of climate observations recorded during collection dates in Todos Santos (by D. R. Sandquist) and weather records for DBG (Tempe, AZ weather station). Thus, it appears that Todos Santos plants at DBG were operating as they would in their native habitat—although A and g values immediately after monsoon rains could have been greater than observed (Table 1), as implied by the high foliage density and Ψ_{pd} values. Nonetheless, throughout this period, growth did continue with substantial A values during September and October (Table 1).

In summary, there did not appear to be any constraints on plant productivity or reproduction during the relatively cooler and wetter spring and summer months at DBG; conditions that are atypical of what *E. farinosa* var. *phenicodonta* would normally experience in Todos Santos. Furthermore, the seasonal changes in Ψ_{pd} , A , g , foliage density and growth were similar to those described for other *E. farinosa* populations within the northern range of this species (Ehleringer 1984, 1985; Comstock et al. 1988; Ehleringer and Cook 1990; Monson et al. 1992; Sandquist 1995). These results demonstrate that a high degree of physiological and phenological adaptability exists for these plants, which may explain, in part, the persistence of isolated *E. farinosa* var. *phenicodonta* populations within the northern range of this taxon. This also suggests that even the "biologically isolated" Cape region of Baja (Shreve 1937) has not given rise to physiologically insurgent populations of *E. farinosa* var. *phenicodonta*. Hence, if there is genetic differentiation for the above mentioned physiological traits, this apparently does not re-

TABLE 2. SUMMARY OF FREEZE DAMAGE TO TODOS SANTOS *ENCELIA FARINOSA* VAR. *PHENICODONTA* PLANTS OVER WINTER 1993–1994 (SEE TEXT FOR RANK METHODS).

	Winter 1993–1994 freeze damage index (number of plants per rank)					Average rank
	0 Killed	1 Extreme	2 Major	3 Moderate	4 Minor	
Todos Santos plants	1	19	0	0	0	0.95
Oatman plants	0	0	5	6	9	3.20

strict the species northern distribution, nor would it be implicated for doing so during past or future climate changes.

Winter freezes. All plants suffered freeze damage in the winters of 1992–1993 and 1993–1994. In 1992–1993, an average of 92.0% (± 3.5) of apical meristems were killed per plant, and there was a positive correlation between plant size and the degree of apical meristem damage (Kendall $\tau = 0.40$, $P < 0.05$). Thus, being of larger size, which was shown to be beneficial for reproduction (above), appears to be detrimental under freezing conditions. As Todos Santos plants would not normally experience freezing temperatures, selection based on this size/intolerance relationship appears to have been relaxed.

In the following winter one plant was killed and all others suffered “extreme” freeze damage (rank = 1) with the death of all stems (Table 2). By comparison, the mean rank for the twenty *E. farinosa* var. *farinosa* plants from Oatman, AZ was 3.2, or just better than “moderate damage” with less than 50% of existing stems being killed (Table 2). This difference clearly points to a mechanism that may limit the northern expansion of *E. farinosa* var. *phenicodonta*, at least for those that are genetically similar to the Todos Santos plants. It also supports the hypothesis proposed by Kyhos (1971), that *E. farinosa* var. *phenicodonta* populations in Arizona, California and parts of Sonora are relicts of a warmer and possibly wetter past climate.

Although there is evidence that summer temperatures in the Mojave and Sonoran Deserts were warmer 6000–9000 ybp (Spaulding and Graumlich 1986), it is not known if winter or annual temperatures were warm enough in the past to sustain populations of freeze-susceptible plants. Other observations, however, lend some support to the “relict populations” hypothesis. Van Devender et al. (1987) showed that the presence and abundance of *E. farinosa* in the Southwest has widely fluctuated since the late Wisconsin period (10,500 ybp). Climatic changes that affected the broad-scale floristic changes described in their study may have also influenced the distributions of *E. farinosa* varieties (Fig. 1). A different study based on a shorter

time scale described the reinvasion of *E. farinosa* into regions of Grand Canyon where the species was very rare, or absent, 100 years ago (Webb and Bowers 1993). This reinvasion, and that of other frost susceptible plants, was attributed to a decreased frequency of freezing temperatures since the late 1800's.

Presently the northern distribution of *E. farinosa* var. *phenicodonta* is within a region where freezing temperatures are common, however, freezing conditions can be spatially patchy (Jones 1978; Bowers 1981). The existence of warm microhabitats within these regions may provide a refuge for *E. farinosa* var. *phenicodonta*. This mechanism has also been proposed as the means by which very isolated individuals of *E. farinosa* and other freeze susceptible species persisted in Grand Canyon after the very cold late-1800's (Webb and Bowers 1993; see also Jones 1978). Indeed, Turnage and Hinckley (1938) reported that after a severe freeze in 1937, damage to *E. farinosa* plants was related to microhabitat, and especially to the distance above canyon or drainage bottoms where ground inversions cause very low temperatures.

CONCLUSION

The study of physiological plasticity outside of the realm of normal climatic conditions is important for understanding the genetic capacity of plants to tolerate climatic changes. With the exception of freeze intolerance, our results suggest that *E. farinosa* var. *phenicodonta* from lower Baja California has the physiological capacity for high productivity under cooler and wetter spring conditions found in its northern range. For these physiological traits it appears that there are few constraints that would preclude this taxon from exploiting pending climate changes. Thus with the possibility of a decrease in the frequency of freezing temperatures, the continuation of global warming, and a potential increase in summer monsoon rainfall (Schlesinger and Mitchell 1987), the conditions for a broader distribution of *E. farinosa* var. *phenicodonta* in the Mojave and Sonoran deserts are imminent.

ACKNOWLEDGMENTS

We thank David Williams, Will Pockman and Omar Lopez for comments on an early version of this manuscript. Craig Cook, K. d., for carbon isotope analyses, and Steve Klassen, Will Pockman, Roland Sandquist and Nancy Burman for field assistance. Will Spangler provided aid in accessing La Paz weather data. D.R.S especially thanks Joseph McAuliffe, Robert Breunig and the staff at the Desert Botanical Garden in Phoenix for assistance and generosity. This research was supported by a Sigma Xi Grant-in-aid of Research and a National Institute of Health training grant in genetics to D.R.S., and a Department of Energy research grant to J.R.E.

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APPENDIX 1

A non-destructive estimate of individual canopy leaf area based on the following equation,

$$\text{canopy leaf area (m}^2\text{)} = \frac{S}{90000} * \sum_{i=1}^3 \left[L_i * \left(\left(0.106 * \sum_{j=1}^3 w_{ij} \right) + \left(0.006 * \sum_{j=1}^3 w_{ij}^2 \right) \right) \right]$$

S is the total number of stems, L_i is the number of leaves for stem i , and w_{ij} is the leaf width (mm) for leaf j of stem i . Three stems ($i = 1, 2, 3$) per plant and three leaves per stem ($j = 1, 2, 3$) were subjectively chosen to represent the diversity of stems on the plant and leaves on each stem. The denominator (90,000) is the product of denominators from $L/3$ (each leaf, j , representing one-third of the leaves on a stem), and $S/3$ (each stem, i , representing one-third of the stems on a plant), and the conversion for cm^2 to m^2 (10,000). The coefficients 0.106 and 0.006 are based on a binomial regression for the conversion of leaf width (mm) to leaf area (cm^2) with the intercept set to zero. This regression ($R^2 = 0.985$; $P < 0.001$) was based on measurements of leaf widths and areas for 762 leaves collected in spring 1992.

This non-destructive estimate appears to be robust, and all values fall between estimates made by two other methods based on: an LAI-2000 plant canopy analyzer (LiCor Inc., Lincoln, NE), and a destructive sample where plant leaves were removed and measured for canopy area (Sandquist 1995).